

Sulfur mediated heavy metal biogeochemical cycles in coastal wetlands: From sediments, rhizosphere to vegetation

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HIGHLIGHTS

- In sediments, the transformation of sulfides may lead to the release of heavy metals.
- In the rhizosphere, sulfur regulates the uptake of heavy metals by plants.
- In plants, sulfur mediates a series of heavy metal tolerance mechanisms.
- Explore interactions between sulfur and heavy metals on different scales is needed.

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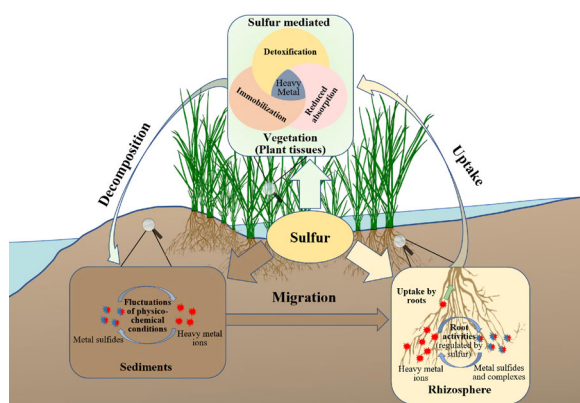
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GRAPHIC ABSTRACT



ABSTRACT

The interactions and mechanisms between sulfur and heavy metals are a growing focus of biogeochemical studies in coastal wetlands. These issues underline the fate of heavy metals bound in sediments or released into the system through sediments. Despite the fact that numerous published studies have suggested sulfur has a significant impact on the bioavailability of heavy metals accumulated in coastal wetlands, to date, no review article has systematically summarized those studies, particularly from the perspective of the three major components of wetland ecosystems (sediments, rhizosphere, and vegetation). The present review summarizes the studies published in the past four decades and highlights the major achievements in this field. Research and studies available thus far indicate that under anaerobic conditions, most of the potentially bioavailable heavy metals in coastal wetland sediments are fixed as precipitates, such as metal sulfides. However, fluctuations in physicochemical conditions may affect sulfur cycling, and hence, directly or indirectly lead to the conversion and migration of heavy metals. In the rhizosphere, root activities and microbes together affect the speciation and transformation of sulfur which in turn mediate the migration of heavy metals. As for plant tissues, tolerance to heavy metals is enhanced by sulfur-containing compounds via promoting a series of chelation and detoxification processes. Finally, to further understand the interactions between sulfur and heavy metals in coastal wetlands, some major future research directions are proposed.

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1 Introduction

Coastal wetlands provide a critical interface between terrestrial and marine habitats and are among the most productive systems on Earth (Liu et al., 2010; Li et al.,

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2017). In the past few decades, with increasing human activities, such as industrial developments and mining, coastal wetlands have suffered serious and multiple environmental issues (e.g., heavy metal contamination) (Table 1 and Table 2). Most heavy metals are primarily stored in anaerobic sediments in the form of insoluble phases, like metal sulfides (Rickard and Morse, 2005; Zhang et al., 2014; Sun et al., 2015; Gao et al., 2016). There are two major pathways for these non-bioavailable heavy metals in the sediments to transform and migrate to other components of wetland ecosystems, such as pore water, rhizosphere, sediment surface, and water column (Fig. 1). One is via changes of pH and Eh in the sediments and sulfur mediated heavy metal biogeochemical cycles (Liu et al., 2010; Rickard et al., 2017); the other is through plant root uptake and litter decomposition (Shi et al., 2019; Costa-Böddeker et al., 2020).

Sulfur, a common biogenic element, plays a vital role in the speciation, transformation, and migration of heavy metals in sediments, which greatly affects the fate of heavy metals, i.e., either they are stored in the sediments or released to pore water and water column (Man et al., 2004; Joseph et al., 2019; Zhang et al., 2020). In anaerobic sediments, heavy metal oxides are reduced and tend to combine with S^{2-} to form metal sulfides with relatively low solubility (e.g., at 25°C K_{sp} of CdS = 8×10^{-28} , K_{sp} of CuS = 6×10^{-37} and K_{sp} of PbS = 3×10^{-28}) and bioavailability (Rickard et al., 2017; Gao et al., 2020). On the other hand, environmental fluctuations (e.g., pH, Eh) may cause metal sulfides oxidation, releasing heavy metals back to the environment (Liu et al., 2010). Also, the increasing fluctuations in the sulfur pool of sediments may cause more heavy metals to be immobilized (Fan et al., 2010). In plant tissues, sulfur regulates the immobilization and detoxification of heavy metals by mediating the speciation, transformation, and

migration of heavy metals (Li et al., 2017; Cao et al., 2018; Wu et al., 2020). Therefore, sulfur is an important factor in studies focusing on the biogeochemical cycles of heavy metals in coastal wetlands, it is imperative to clarify the interactions and mechanisms between sulfur and heavy metals, especially in the context of their speciation, transformation, and migration in coastal wetlands.

Numerous biogeochemical cycles of different elements, including heavy metals and sulfur, occur or operate at different organizational levels of wetlands (Zhou et al., 2011; Thomas et al., 2014), e.g., sediments, rhizosphere (a micro-interface between sediments and plants), and vegetation. Both heavy metals and sulfur migrate in the path of sediments-rhizosphere-vegetation and subsequently back to sediments (Wang et al., 2013; Li et al., 2017; Zhang et al., 2021). The processes and characteristics of the interactions may differ at each of the three organizational levels (Zhou et al., 2011; Gao et al., 2016; Pardue and Patrick, 2018).

To the best of our knowledge, although there have been several studies focusing on the interactions between sulfur and heavy metals in coastal wetlands, there are currently no review articles that systematically summarized them, particularly from the perspective of three components of wetland ecosystems. Thus, we conducted a detailed review of the studies on the interactions between sulfur and heavy metals in coastal wetlands published in the past four decades and summarized the information based on sediments, rhizosphere, and vegetation. First, we reviewed the current progress of knowledge on heavy metal and sulfur biogeochemical cycles. Then, we focused on how sulfur mediates speciation, transformation, and migration of heavy metals among sediments, rhizosphere, and vegetation. Finally, we proposed some major future research directions.

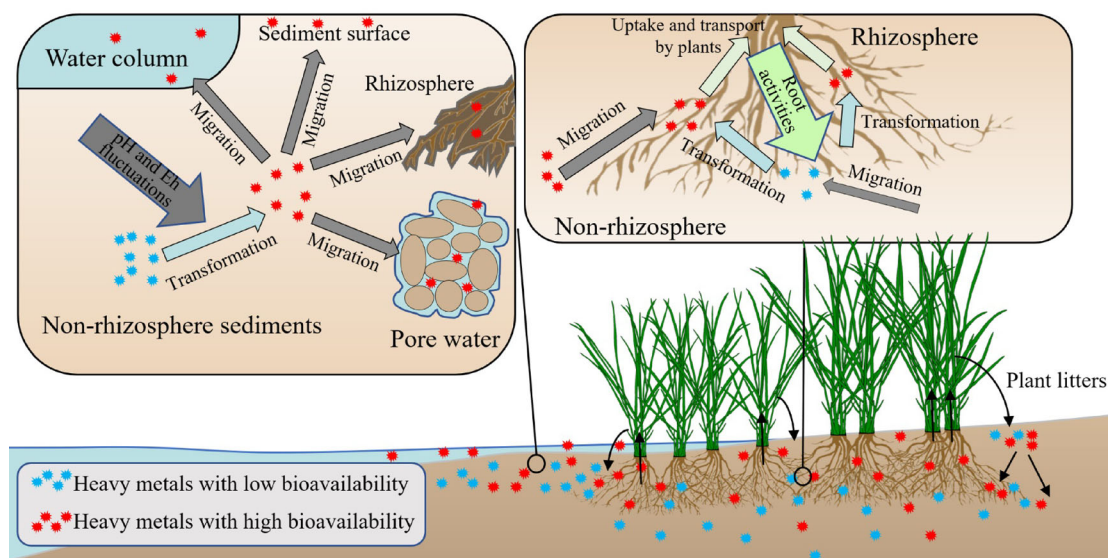


Fig. 1 The transformation and migration of heavy metals in the coastal wetland ecosystem.

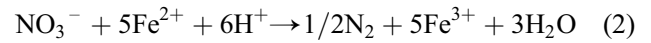
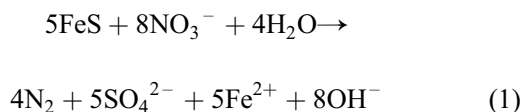
2 Sulfur and heavy metals in coastal wetlands

Sulfur is a crucial biogenic element that widely distributed in nature. Major sources of sulfur in coastal wetlands include anthropogenic activities (such as sewage, acid rain, fertilizer), material exchange caused by natural tides, and sediment decomposition. In general, most sulfur compounds need to be transformed to inorganic states (sulfide, sulfate), usually through microbial and plant root activities, to be available for plant utilization and participate in the biogeochemical cycle of multiple elements (Edwards, 1998). Therefore, the oxidation of sulfide and the reduction of sulfate together are considered as a “bridge” that connects microbes, sediments, and plants.

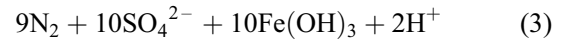
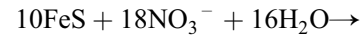
Generally, the concentration of heavy metals in nature is relatively low. However, in the last few decades, with the development of industry and mining, large amounts of heavy metals were introduced into estuarine and coastal zones through rivers, groundwater, and atmospheric deposition. Thus, coastal wetlands have become a natural “habitat” for heavy metals (Doyle and Otte, 1997; Zhang et al., 2007). Heavy metals in sediments can transfer to rivers and oceans with natural tides. Besides, heavy metals may cause a series of damages to wetland plants and eventually result in plant growth retardation and low biomass (Yadav, 2010; Chai et al., 2014a). Wetland plants uptake and store heavy metals in their tissues, and these stored heavy metals may then be transferred to the food chain, accumulating over time and may ultimately pose a risk to human health (Hempel et al., 2008). Thus, coastal wetlands are considered to be both a “sink” and a “source” of heavy metals.

2.1 Biogeochemical cycle of sulfur in coastal wetlands

In coastal wetlands, the biogeochemical cycle of sulfur mainly includes sulfur oxidation and sulfate reduction (Fig. 2). Sulfur oxidation is a process in which sulfides, elemental sulfur, and other reduced sulfur are oxidized (Tourova et al., 2010). In anaerobic sediments, sulfur oxidation is generally mediated by sulfur-oxidizing bacteria (SOB) that utilize nitrate as an electron acceptor (Yang et al., 2017; Guo et al., 2020). In this process, the reduced sulfur is ultimately oxidized to sulfate and nitrate is reduced to N_2 (Zhang et al., 2019b). Taking the most common sulfide mineral in sediments, ferrous sulfide (FeS) (Rickard, 2017; Hu et al., 2020), as an example, SOB oxidize sulfide while reducing nitrate through the following pathway (Li et al., 2016c):



The overall reaction can be expressed as the following equation:



In addition to promoting the biogeochemical cycle of sulfur, as reviewed by Hu et al., (2020), in anaerobic environments, the oxidation of FeS and simultaneous denitrification processes mediated by SOB play critical roles in linking the cycles of sulfur, nitrogen, iron, and other biogenic elements. Besides, the distribution of SOB was reported to be stimulated by radial oxygen loss (ROL), litter decomposition, and root exudates of plants. Therefore, SOB is mainly distributed in the rhizosphere, where root activity is very high (Zheng et al., 2017). For example, *Spartina alterniflora* was reported to promote SOB activity in sediments (Thomas et al., 2014), and higher transcriptional activity of SoxB was obtained in the rhizosphere of *Kandelia obovata* than that of mudflats (Li et al., 2021). Additionally, some plants can directly oxidize sulfides. According to a previous study, in a mangrove forest in Fujian Province, China, the ROL of roots facilitates the oxidation of pyrite, leading to the release of sulfate and increasing the acidity of sediments (Deng et al., 2019).

In coastal wetlands, the reduction of oxidized sulfur includes assimilatory reduction and dissimilatory reduction (Fig. 2). In the assimilatory reduction process, inorganic sulfur is reduced by plants and microbes. Cysteine, methionine, and other sulfur-containing amino acids are synthesized through a series of processes catalyzed by enzymes in plants. Cysteine is the first amino acid synthesized by plants and an essential precursor of numerous biomolecules (Takahashi et al., 2011). The thiol group ($R-S^-$) in cysteine is relatively reactive and closely related to the structure and folding of proteins that directly affect its stability and function (Haag et al., 2012). Methionine is also a precursor of many biological macromolecules and a key amino acid for protein synthesis (Romero et al., 2014). In addition, some salt marsh plants can also synthesize “special” sulfur-containing compounds (e.g., Dimethylsulfoniopropionate, also known as DMSP) (Rousseau et al., 2017). In *S. alterniflora*, DMSP not only regulates osmotic pressure and maintains the stability of the intracellular environment, but also acts as an antioxidant, scavenging heavy metal-induced reactive oxygen species (ROS). In previous research on *S. alterniflora*, the ratio of DMSO (dimethylsulfoxide) to DMSP and foliar metals together were considered to be accurate and effective when assessing the degree of environmental stress, the DMSO/DMSP ratio

was higher under stress, owing to the oxidative stress and disturbances caused by heavy metals (McFarlin and Alber, 2013). As mentioned above, *S. alterniflora* synthesizes and stores DMSP in plant tissues, and the decomposition of litter and residues may lead to increased sulfur storage in the sediment. As a result, DMSP is seen a “chemical weapon” that aids invasive species in competing with native plants (Xia et al., 2015; Luo et al., 2019).

In sediments, sulfide is mainly derived from SRB activities. About 288 million tons of sulfide are produced annually in sediments and associated waters through SRB activities (Rickard et al., 2017). Additionally, in sediments, SRB-mediated reduction is also one of the most important pathways of organic mineralization (Jørgensen, 1982; Roychoudhury et al., 2013), in which process, the organic matter as the electron donor is oxidized and the sulfate as the electron acceptor is reduced (Singleton, 1993; Barton and Fauque, 2009). Previous studies have shown that in coastal wetlands, anaerobic mineralization of organic matter is achieved mainly through methanogenesis and sulfate reduction. In such processes, methanogenic bacteria and SRB compete for substrates (hydrogen and acetate, etc.) as electron donors, while SRB utilizes a variety of organic matter as substrates and therefore have a higher affinity (Nedwell et al., 2004). In a coastal wetland dominated by *S. alterniflora*, the abundance of SRB was

two orders of magnitude higher than methanogenic bacteria (Zeleeke et al., 2013). This was consistent with the findings of Pallud and Van Cappellen (2006) and Pester et al. (2012), who found that the major pathway for anaerobic mineralization of organic matter in coastal wetlands is sulfate reduction.

2.2 Heavy metals in coastal wetlands

As previously stated, coastal wetlands are both a “sink” and a “source” of heavy metals. Human activities have impacted or contaminated coastal wetlands around the world to varying degrees (Table. 1). Heavy metals induced by human activities and natural processes are concentrated in sediments in various chemical speciation. Some of these heavy metals are in relatively stable speciation (complexed with large organic molecules, adsorbed or occluded by precipitated oxides, etc.), while water-soluble and exchangeable heavy metals could migrate into water and wetland plants through a series of transformations (Du Laing et al., 2009). Coastal wetland sediments are typically divided into aerobic layers, aerobic-anaerobic interfaces, and anaerobic layers. In the surface oxidizing environment, heavy metals tend to co-precipitate or bind to oxides. The binding level of heavy metals to oxides tends to be increased with the increase of sediment oxidation

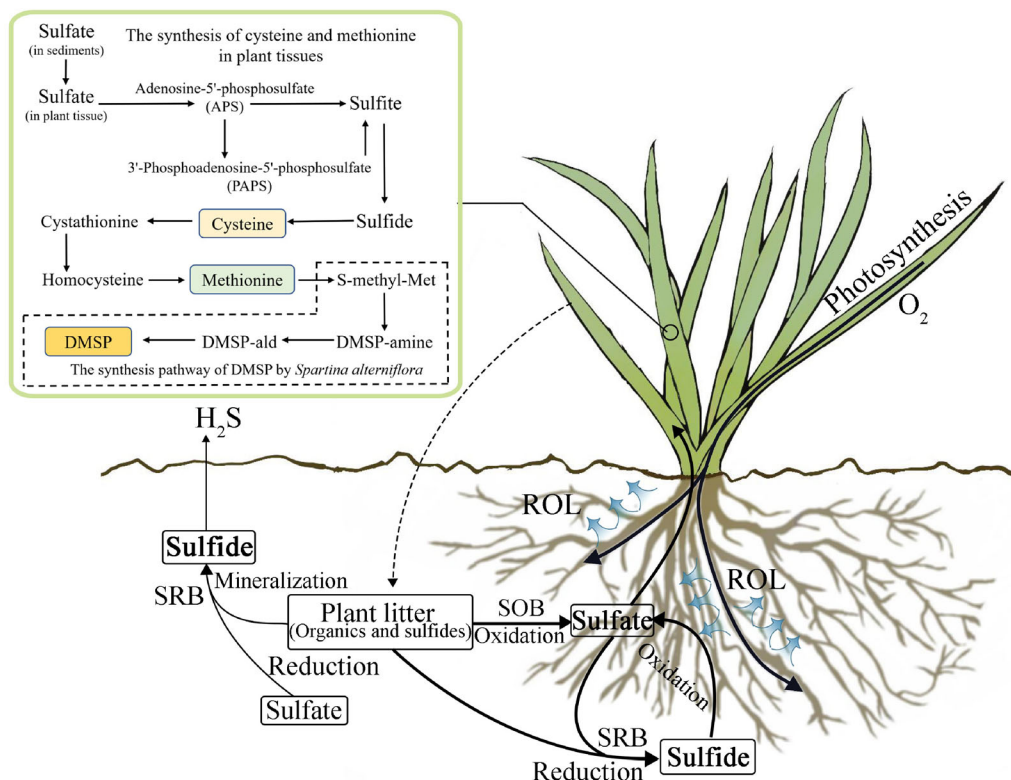


Fig. 2 The sediment-plant cycle of sulfur in coastal wetlands.

Table 1 Heavy metal concentration of different coastal wetlands in the world (mg/kg)

Locations	Value	Cd	Cr	Cu	Ni	Pb	Zn	Reference
Futian Mangrove, Shenzhen, China	Range	5.35–6.18	34.83–71.84	79.22–84.98	101.03–148.88	NA	324.48–401.03	Wu et al., 2019
	Mean	5.70	49.76	82.62	117.92		351.15	
Xixiang Mangrove, Shenzhen, China	Range	8.33–9.08	96.42–116.06	328.63–431.83	157.86–176.04	NA	354.83–497.43	Wu et al., 2019
	Mean	8.76	103.09	381.56	168.12		429.41	
Shajing Mangrove, Shenzhen, China	Range	7.63–8.32	299.05–317.66	1547.66–1624.34	366.59–424.50	NA	632.28–658.95	Wu et al., 2019
	Mean	7.98	311.16	1595.24	397.87		649.19	
Dongzhaigang Mangrove, Hainan, China	Mean	0.96	65.77	15.37	18.97	19.32	48.57	Shi et al., 2019
Zhanjiang Mangrove, Guangdong, China	Mean	1.74	71.53	20.95	21.85	37.01	76.60	Shi et al., 2019
Yellow River Estuary, China	Range	NA	35.9–54.7	15.6–29.9	17.6–28.4	35.8–51.7	38.2–68.3	Sun et al., 2015
	Mean	NA	44.09	22.85	22.97	43.05	54.12	
Bohai Bay, China	Mean	8.21	NA	50.06	NA	48.12	893.63	Chai et al., 2014b
Min River Estuary, China	Range	NA	33.3–128.9	23.2–74.4	16.7–61.9	17.8–159.0	71.6–267.4	Sun et al., 2017
	Mean	NA	73.8	41.2	33.7	62.3	146.6	
Subei Shoal, Jiangsu, China	Mean	0.56	19.22	11.32	47.88	0.13	38.18	Zhang et al., 2019a
Yangtze Estuary, China	Mean	0.15	87.17	25.51	32.24	24.18	84.91	Liu et al., 2016
Pearl River Estuary, China	Mean	2.38	109.7	65.36	50.36	79.27	244.42	Zhang et al., 2010
Can Gio Biosphere Reserve, Vietnam	Range	0.01–0.2	27.1–71.5	7.1–27	11.7–56.3	8–20.4	25.7–108.1	Costa-Bôddeker et al., 2020
	Mean	0.06	51	17	29	15	57	
Seine Estuary, France	Range	NA	NA	3–45	18–43	18–78	53–188	Cundy et al., 2005
	Mean	NA	NA	29	27	48	123	
Medway Estuary, UK	Mean	NA	76	42	28	67	138	Spencer, 2002
Pozo Salt Marsh, Patagonia, Argentina	Range	0.32–0.77	37.39–86.13	4.42–6.8	12.11–32.54	7.14–14.55	15.44–24.95	Idaszkin et al., 2020
Parnaiba River Delta Estuary, Brazil	Mean	0.51	62.64	5.31	23.29	10.28	19.89	
	Range	NA	1.5–38	1.5–14	NA	1.5–11	2.6–23	de Paula Filho et al., 2015
Sediment Quality Guidelines of China	Mean		18.0	6.8		5.9	13.4	
	Class I	0.50	80.0	35.0	NA	60.0	150.0	SEPA, 2002
	Class II	1.50	150.0	100.0		130.0	350.0	
	Class III	5.00	270.0	200.0		250.0	600.0	

NA = not available.

(Guo et al., 1997), while the decomposition of oxides due to reduced redox potential might cause the release of heavy metals (O'Geen et al., 2010). In contrast, in the deeper anaerobic layers, heavy metals generally exist in the form of insoluble phases like sulfides (Rickard et al., 2017), whereas the fluctuation of Eh and pH may lead to the transformation and migration of heavy metals.

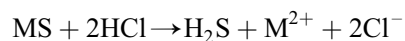
In the coastal wetland ecosystem, plants directly or indirectly affect the speciation and migration of heavy metals and hence, may increase the activity of heavy metals in sediments. In the study of Zhou et al. (2011), the root activity of mangrove plants decreased the pH of sediment, which caused the leaching of heavy metals. Moreover, changes in sediment pH and Eh caused by root oxygen secretion results in the migration of heavy metals were also reported by Pardue and Patrick (2018). Besides, in the study of MacFarlane et al. (2003) on a mangrove, the concentration of Cu and Zn in sediments increased over time due to the ion adsorption of litter and microbial activity. Furthermore, our previous research and other studies have demonstrated that in sediments, high bioavailable forms of heavy metals can be absorbed directly by plant root cells through specific or generic ionophore and channel proteins, and accumulated in plant tissues (Viehweger, 2014; Li et al., 2015; Ghorri et al., 2019). Additionally, microbes also affect the speciation, migration, and bioavailability of heavy metals in sediments. In a Brazilian mangrove forest, the methylation of mercury (Hg) was partially attributed to the activities of sulfate-reducing bacteria (Correia and Guimarães, 2017). In another study, the accumulation of selenium (Se) and Hg in *Scirpus robustus* tissues was decreased after antibiotic inhibition of microbial activity in sediments (De Souza et al., 1999). As the interface between root and sediment, in the rhizosphere, mycorrhiza was reported to absorb and fix heavy metals, and thereby decreasing the uptake of heavy metals by plants and improving its stress tolerance (Hildebrandt et al., 2007). Overall, wetland plants play a “sink-source” function, as they uptake heavy metals from sediments and accumulate them in tissues. These heavy metals accumulated in tissues are further released into the natural environment when they become litterfall.

3 Interaction between sulfur and heavy metals in coastal wetlands

Coastal wetlands are rich in sulfur, an essential element that performs important biological and physiologic functions in plants and animals. The transformation and migration of sulfur is the “bridge” for the interactions among microbes, sediments, and plants in the ecosystem. For example, the speciation, transformation, and migration of heavy metals in sediments; heavy metals migrated to the rhizosphere, absorbed by the root, and redistributed in plant tissues are all closely related to the sulfur cycle.

3.1 Mediation of sulfur on the speciation and migration of heavy metals in sediments

Generally, coastal wetland sediments are anaerobic and reductive (Rickard and Morse, 2005; Rickard et al., 2017). Sulfate reduction may occur in sediments with a redox potential below -100 mV (O'Geen et al., 2010). In this reduction process, sulfates obtain electrons and are reduced to sulfides which could directly bind to metal cations in sediments to form relatively stable metal sulfides. Numerous studies have shown that in anaerobic sediments, the formation of metal sulfides is an important way to immobilize and retain heavy metals. In the study by Harbison (1986) on *Avicennia marina*, sulfate reduction in anaerobic sub-surface sediments was found to contribute to the retention of metals as sulfides. Griffin et al. (1989) reported that in Chesapeake Bay marshes, sulfide precipitation controls the distribution of cadmium (Cd), copper (Cu), nickel (Ni), and zinc (Zn) in sediments. In a greenhouse study, Kerner and Wallmann (1992) simulated the alternate anaerobic and aerobic conditions of intertidal sediments and followed the mobilization of Cd and Zn. Both Cd and Zn were removed from pore water by forming sulfide precipitation during the anaerobic period and released from sediments during the aerobic period. The release of heavy metals under aerobic conditions was attributed to the mineralization of organic matter and sulfide oxidation. In subsequent research, in sediments, the active sulfide was described as acid volatile sulfide (AVS), which is operationally defined as the sulfur convert into H_2S and released by the addition of HCl (Rickard and Morse, 2005):



$$(\text{M} = \text{Metals, MS} = \text{Metal sulfides}) \quad (4)$$

AVS is one of the most active sulfide species in coastal wetland sediments and affects the speciation and migration of heavy metals by forming insoluble and bio-unavailable heavy metal sulfides (Youssef and Saenger, 1998). Due to the presence of radial oxygen loss by plants and the surface atmosphere, the AVS concentration is generally lower in the rhizosphere and sediment surface. Our previous studies have evidenced that root exudates such as phenols and flavonoids secreted by *A. marina* were able to act as antioxidants and promote the formation of AVS. Simultaneously, AVS can bind heavy metals, reduce their bioavailability as well as lead to the decrease of redox potential, which would further stimulate the formation of AVS and increase the AVS concentration in sediments (Li et al., 2015; Li et al., 2016b; Youli et al., 2020). Simultaneously extracted metals (SEM), similar to AVS, are all operationally defined methods for analyzing sulfide and associated metals in coastal wetland sediments (Allen et al., 1993). The SEM/AVS ratio is widely used to

evaluate the bioavailability and potential biotoxicity of heavy metals in sediments. At present, it is commonly assumed that when this ratio is less than 1, there is no potential risk of heavy metal toxicity in the sediments. However, when it is greater than 1, there might be potential toxicity (Chai et al., 2015). Some study results of different coastal areas based on the SEM/AVS method were summarized (Table 2). In the study of Mangrove in Zhangjiang Estuary, China, by Liu et al. (2010), the AVS concentration in forest sediments was lower than that in mudflat sediments. The SEM/AVS ratio might be higher than 1, in which AVS cannot bind all the reactive metals and may be a threat to animals and plants. In the Shenzhen Futian mangrove, the SEM was distributed evenly, while AVS distributions were more variable. The main component of SEM was Zn (69.7%–94.2%), while the highly toxic Cd accounted for less than 1% (Chai et al., 2015). Wang et al. (2015a) showed that AVS concentrations varied with seasons in Yangtze Estuary. Compared with other estuaries, SEM_{Cu} and SEM_{Ni} were abnormally high and had potential toxicities. Similarly, in a study by Shyleshchandran et al. (2018) in Vembanad Lake Estuary Indian, the SEM/AVS ratio varied during seasons. The ratio in post-monsoon, pre-monsoon and monsoon seasons decreased sequentially. In the post-monsoon season, 91% of study sites showed high bioavailability of metals which may result in toxicity to aquatic biota, while 66% of sites showed similar bioavailability in the pre-monsoon season. In a study conducted in Asaluyeh, Iran, AVS concentrations of sediments in the industrial region were greater than those in the urban area due to the discharge of industrial effluents. In the autumn, 20% of sampling stations were reported to have a potential biotoxicity, while in the spring this percentage was increased to 47% (Arfaeina et al., 2016). Nizoli and Luiz-Silva (2012) studied the sediments in the Marrao estuary, Santos-Cubatao, Brazil. They found that the SEM of sediments in the Marrao estuary was not high, but the SEM/AVS ratio was greater than 1 when AVS was low in summer. It reflected the potential biotoxicity and also indicated the priority and importance of the combination of AVS and heavy metals. In summary, the concentration of AVS mainly depends on the sediment redox and pH conditions, mediated by tidal, plant root, and microbial activities, seasonal changes, and human activities.

Additionally, iron sulfides are one of the primary sulfide deposits in wetland and marine sediments (Rickard, 1995; Hu et al., 2020). The formation of iron sulfides is mainly due to the reduction of iron oxides and oxyhydroxides in a reducing environment and is a part of the iron-sulfur cycle, in which the speciation, transformation, and migration of heavy metals are closely associated with iron sulfides (Cutter and Velinsky, 1988; Alongi, 2010; Jiang et al., 2019). In wetland sediments, iron sulfides mainly include ferrous sulfide (FeS), pyrite (FeS₂), and greigite (Fe₃S₄) (Karimian et al., 2018). FeS is a crucial intermediate in the

formation of pyrite, compared with pyrite, the formation of FeS is more rapid (Neretin et al., 2004). In a reducing environment, free Fe²⁺ and hydrogen sulfide (H₂S) form FeS first, and later with the participation of H₂S or S⁰, the FeS can be further reduced to FeS₂ (Rickard, 1975). The formation of pyrite can also be summarized as the reduction of iron oxide to Fe²⁺ under anaerobic conditions and the reduction of sulfate to sulfide catalyzed by SRB, which then together eventually form pyrite (Johnston et al., 2004). Numerous studies showed that iron sulfides could adsorb and fix heavy metals under reducing conditions. Heavy metal nanoparticles were discovered in the matrix of deformed and polycrystalline pyrite using electron microscopy (Deditius et al., 2011). Mackinawite, a kind of nano-crystalline of ferrous sulfide, was also reported to fix heavy metals. For example, Cd and Pb replaced up to 29% of Fe in mackinawite to form sulfides in addition to being directly adsorbed on the surface of mackinawite, according to the study conducted by Coles et al. (2000). Niazi and Burton (2016) found that with the presence of PO₄³⁻, mackinawite can fix 99% of arsenic. Similarly, nickel can also be adsorbed and fixed by mackinawite (Wilkin and Beak, 2017). Moreover, the fluctuation of environmental factors in sediments may cause the oxidation of iron sulfides. As mentioned above, the oxidation of iron sulfides is mainly mediated by SOB, in which sulfides are oxidized to sulfates. The oxidation process promotes the sulfur cycle in sediments. On the other hand, it decreases the pH and increases the acidity of sediments (Li et al., 2016c; Karimian et al., 2018). Therefore, this oxidation process may cause the release of heavy metals that have been adsorbed and fixed by iron sulfides and increase the bioavailability of heavy metals in sediments.

3.2 The interaction between sulfur and heavy metals in the rhizosphere

Compared with sediments, the biogeochemical cycle of various biogenic elements in the rhizosphere microenvironment fluctuates more, and the interaction between sulfur and heavy metals is more complicated due to the effects of roots activities, microbes, and other factors. A large number of previous studies have shown that the presence of plants affects the distribution of heavy metals in coastal wetland sediments, especially in the rhizosphere where plant roots were active (Lacerda et al., 1997; Yang et al., 2010; Chai et al., 2014b; Li et al., 2016a). When plant roots selectively absorb ions from the sediments or some ions freely diffused in the sediments, the concentration gradients would cause the migration of essential and non-essential elements from the non-rhizosphere to the rhizosphere (Peralta-Videa et al., 2009). In previous rhizobox cultivation, we have found that root activities of *K. obovata* significantly increased the reducible heavy metals while reduced acid-extractable and oxidizable heavy

Table 2 Summary of acid-volatile sulfide (AVS) and simultaneously extracted metals (SEM) of different coastal areas in the world

Locations	Value	AVS umol/g	SEM ^a umol/g	SEM _{Cd} umol/g	SEM _{Cu} umol/g	SEM _{Ni} umol/g	SEM _{Pb} umol/g	SEM _{Zn} umol/g	Reference
Zhangjiang Estuary Mangrove, Fujian, China	Range	0.2–12.5	1.4–2.1	0.623–1.690	0.152–0.324	0.095–0.20	0.115–0.197	0.731–1.391	Liu et al., 2010
Futian Mangrove, Shenzhen, China	Mean	2.93	2.37	0.0113	0.13	NA	0.17	2.06	Chai et al., 2015
Pearl River Estuary, South China	Mean	1.59	1.95	0.0430	0.31	0.29	0.18	0.94	Fang et al., 2005
Coastal Areas of Leizhou Peninsula, China	Range	0.11–55.55	0.03–8.60	0.03–0.826	0.001–0.161	0.001–0.069	0.001–0.185	0.02–8.21	Li et al., 2014
	Mean	4.451	0.843	0.146	0.031	0.01	0.045	0.757	
Yangtze River Estuary, China	Range	0.0016–8.5	0.326–7.3	0.00024–0.005	0.0246–2.56	0.029–5.96	0.014–0.203	0.114–1.36	Wang et al., 2015a
	Mean	0.86	1.163	0.0013	0.266	0.36	0.069	0.467	
Yellow River Estuary, China	Range	0.15–0.185	0.90–1.86	0.184–0.376	0.212–0.404	NA	0.017–0.033	0.438–1.228	Wu et al., 2007
	Mean	0.94	1.33	0.022	0.289		0.230	0.764	
Bohai Bay, China	Range	0.39–3.99	0.54–1.46	0.0002–0.0017	0.091–0.308	0.096–0.273	0.037–0.099	0.289–0.782	Gao et al., 2020
	Mean	1.25	1.05	0.0007	0.211	0.192	0.071	0.572	
Vembanad Lake Estuary, India	Range	0.10–3.31	0.09–7.17	0.00–0.09	0.01–0.56	NA	0.00–0.06	0.00–7.12	Shyleshchandran et al., 2018
	Mean	1.15	1.30	0.02	0.15		0.02	1.13	
Pialassa Piomboni Coastal Lagoon, Italy	Range	0.03–8.8	0.3–6.6	0.001–0.007	0.005–1.4	0.04–0.3	0.02–0.2	0.2–6.1	Pignotti et al., 2018
	Mean	3.1	1.7	0.003	0.1	0.2	0.06	1.4	
Asaluyeh Harbor, Iran	Range	0.017–22.74	0.22–20.15	0.0005–0.0098	0.09–6.34	0.005–0.034	0.009–1.14	0.13–12.43	Arfaeinia et al., 2016
	Mean	4.63	7.72	0.22	1.86	0.0026	0.39	4.44	
Manzalah Lagoon, Egypt	Mean	26.13	2.894	0.008	0.411	0.211	0.175	2.089	Younis et al., 2014
South Coast of São Paulo, Brazil	Mean	2.83	1.71	0.0035	0.185	0.085	0.166	1.270	Nizoli and Luiz-Silva, 2012

NA = not available; ^a The sum of the SEM_{Cd}, SEM_{Cu}, SEM_{Ni}, SEM_{Pb} and SEM_{Zn}.

metals (Li et al., 2016a). Besides, another study on *S. alterniflora* marshes and mudflats showed that the heavy metal concentration in the *S. alterniflora* marsh (5–15 cm depth) was four times higher than that in mudflats (Lacerda et al., 1997). In Bohai Bay, China, a similar result was obtained by Chai et al. (2014b) that *S. alterniflora* marsh may have a higher heavy metal concentration than mudflats. Oxygen excretion from plant roots would affect the redox conditions in the rhizosphere, which in turn affect the presence of sulfides and the speciation of heavy metals (Yang and Ye, 2009). In the study of Liu et al. (2010), compared with mudflats, the AVS of mangrove sediments was significantly lower due to plant root activities, and this phenomenon was pronounced at the 15–45 cm depth where the root activity was the highest, and the amount of AVS was too low to bind all the reactive metals as sulfides. Another study reported that the rhizosphere of waterlogged sediments had a higher soluble iron concentration and higher Eh when compared with mudflats (Wright and Otte, 1999). Radial oxygen loss by *S. alterniflora* roots was observed to affect the AVS concentration and the conversion of pyrite and ferric oxides in the rhizosphere, and hence, mediate the formation of iron plaque (Kostka and Luther, 1995; Zhang et al., 2021). Iron plaque is the first physical barrier for heavy metals to enter the root from the rhizosphere. In the study conducted by Lin et al. (2018), the addition of 20 mM Na_2SO_4 (as a sulfur amendment) significantly promoted the oxygen release from the root aerenchyma and significantly increased the concentration of DCB-extractable iron in the rhizosphere, and finally enhanced iron plaque formation. With the “fence effect” and adsorption effect, the iron plaque effectively decreased the absorption of heavy metals in plant roots. Similarly, our previous research on mangroves also found that sulfur promoted the formation of iron plaque on the root surface of *K. obovata* (Li et al., 2016a; Li et al., 2017). For rice, sulfur supply significantly enhanced the formation of iron plaque and alleviated the accumulation of Cd in plant tissues (Cao et al., 2018). Besides, plant root exudates, such as phenols and flavonoids, may act as antioxidants, as previously indicated. In contrast, some other plant root exudates, like low molecular weight organic acids, were reported to decrease the pH of sediments (Lu et al., 2007; Xie et al., 2013), thereby affecting the speciation and migration of sulfur, changing the transformation and migration of heavy metals.

The activities of SRB are not only associated with the biogeochemical cycle of sulfur, but also directly affect the speciation, transformation, and migration of heavy metals. In general, the presence of SRB mediates the formation of heavy metal sulfides and fixes them to reduce their biotoxicity (Lin et al., 2010; Niu et al., 2018; Li et al., 2019b). In a study conducted by Niu et al. (2018), the SRB abundance in the rhizosphere of *Scirpus triquetus* was significantly higher than those in the non-rhizosphere, and

the majority of metals were immobilized by the SRB in the rhizosphere. However, many bio-derived metal-sulfide nanoparticles were found both in the rhizosphere and tissues of *S. triquetus*, indicating the potential bioavailability of the nanoparticles. It was further reported that in the rhizosphere of *S. triquetus*, SRB significantly improved the absorption of Ag^0 -nanoparticles by transforming them into Ag-sulfide nanoparticles (Niu et al., 2020). The higher absorption was attributed to the size of nanoparticles smaller than 10 nm, which can be effectively absorbed by plants and accumulated in tissues, causing biotoxicity and may transfer via the food chain (Wang et al., 2015b). In recent years, metal-containing nanoparticles have been found in various environments and are considered to be a new type of contamination. However, previous studies have mainly focused on the effects of metal oxide nanoparticles on terrestrial plants (Du et al., 2017; Yang et al., 2021), whereas research on metal sulfide nanoparticles in wetland plants is scarce. Coastal wetland sediments are relatively anaerobic, reductive, and rich in sulfide. Hence, further research should focus on the transformation and migration of metal sulfide nanoparticles (especially highly toxic heavy metals), elaborate the role of SRB in this process and further reveal the biogeochemical behavior of sulfur and heavy metals under the coupling of microbes and plants at the microscopic level. Moreover, studies are urgently needed to evaluate the toxicological effects of these nanoparticles on plants and the potential risks to other organisms caused by their bioaccumulation via the food chain.

For wetland plants, iron plaque formation through radial oxygen loss has been widely studied and recognized as the main cause of heavy metal sequestration in the rhizosphere. However, the contribution of microbes to heavy metal fixation in the rhizosphere is not fully understood. In previous studies, various microbes were found in the rhizosphere and rhizoplane of plants, mainly sulfur-oxidizing bacteria (SOB), sulfate-reducing bacteria (SRB), iron-oxidizing bacteria (FeOB), and iron-reducing bacteria (FeRB) (Chi et al., 2018; Zecchin et al., 2019; Zhang et al., 2021). As shown in Fig. 3, the current hypothesis suggests that the rhizoplane biofilm structure mainly includes an aerobic inner layer and an anaerobic outer layer (Li et al., 2019b), which is due to the oxygen diffusion caused by ROL and induces a decreasing gradient from the root surface to the sediments (Yamaguchi et al., 2014). Because of the gradient of redox conditions, SRB, SOB, and other microbes are distributed in this heterogeneous biofilm (Stewart and Franklin, 2008). In the inner aerobic area, with the presence of ROL, pyrite is oxidized by SOB, then Fe^{2+} is further oxidized by FeOB to form goethite and ferrihydrite, both of which are the main components of iron plaque (Hansel et al., 2001). Meanwhile, the oxygen supply decreases with increasing distance from the rhizoplane in the outer layer and forms an anaerobic layer, in this anaerobic area, SO_4^{2-} diffused

from the oxidizing area is reduced to S^{2-} by SRB. As mentioned above, root activities may cause the migration of heavy metal ions from the non-rhizosphere to the rhizosphere. Due to the low solubility of metal sulfides, heavy metal ions can easily form metal sulfide precipitations with S^{2-} when heavy metal ions reach the biofilm's outer reducing area. Therefore, most heavy metal ions are immobilized and fixed in the outer layer of the biofilm. However, the structure of the biofilm still needs to be confirmed as well as microbial community composition. The interactions among the iron plaque, microbes, and heavy metals are still unclear. To reveal the biogeochemical behavior of sulfur and heavy metals in the rhizosphere, and the sediments-plant micro-interface, further studies should focus on determining the composition, structure, and characteristics of the heterogeneous biofilm and elaborating the interaction among sulfur, iron, and heavy metals mediated by microbes and plants.

3.3 Effects of sulfur on the tolerance and detoxification of heavy metal stress in plants

In plants, compared with sediments and rhizosphere, the interactions between sulfur and heavy metals are different. In sediments and rhizosphere, sulfur mediated the speciation, transformation, and migration of heavy metals, together with other factors such as microbes and root exudates. However, in plants, sulfur directly or indirectly mediated the uptake, transformation, and translocation of heavy metals via different physiologic and metabolic pathways. When different heavy metals enter plants, their transformation and migration mechanisms are also different (Fig. 4). Arsenic is a kind of metalloid element with biotoxicity due to its chemical similarity with phosphate. As(V) is absorbed and transported through phosphate transport channels (Tripathi et al., 2007). In plant tissues, As(V) is reduced to As(III), which has less mobility but is

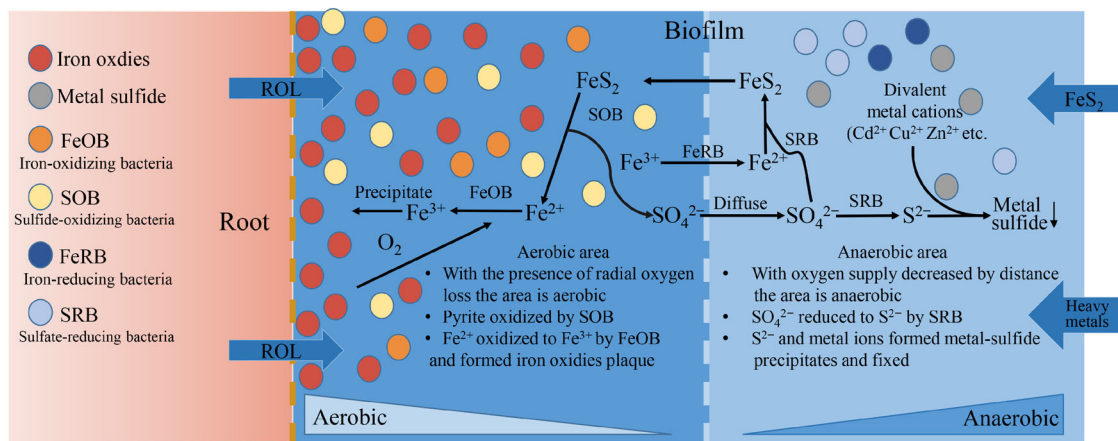


Fig. 3 A conceptual model of biofilm and metal-sulfur cycle in the rhizosphere of root (*Figure adapted from Li et al., 2019b).

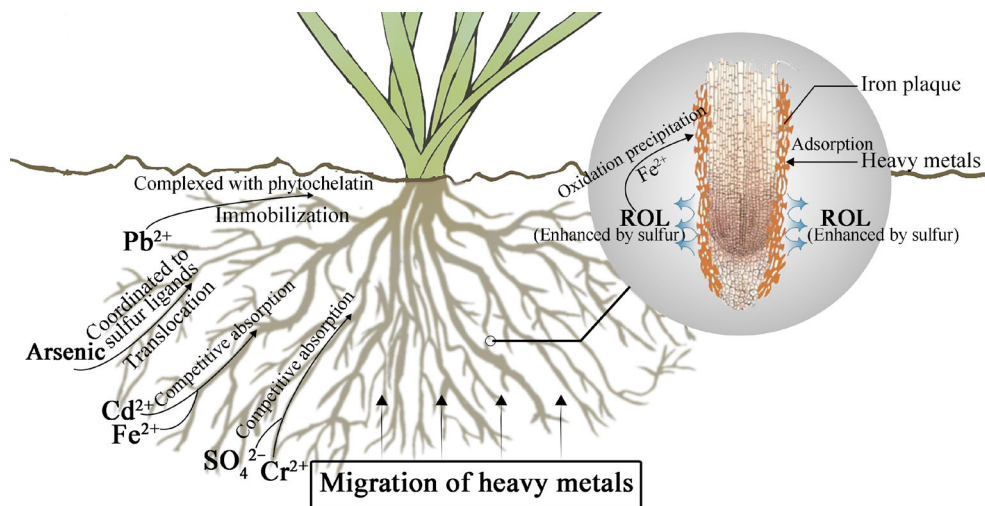


Fig. 4 The mediating role of sulfur in plant absorption and transport of heavy metals from the rhizosphere.

more toxic (Dhankher et al., 2012). Meanwhile, As(III) can form complexes with various organic acids and also form As-sulfur complexes with thiolate ligands and transported in the form of As(III)-tris-glutathione complex (Peralta-Videa et al., 2009; Kumar et al., 2019). Due to their high affinity with As(III), thiol-containing compounds may reduce As translocation, and As(III)-thiol complexation is considered to play a key role in the immobilization of inorganic As species (Kumarathilaka et al., 2018). Cadmium is a highly toxic heavy metal with very low natural concentrations. However, due to human activity such as industrial production, it is released into the environment, causing some serious environmental hazards. The electrochemical potential gradient of the plasma membrane drives Cd into root cells (He et al., 2017). As mentioned above, Cd competes with other cations for ion carriers or channels to enter the cell, such as Ca and Fe channels. Chai et al. (2013) reported that an increase in the Ca^{2+} concentration in sediments significantly decreased the absorption of Cd by *S. alterniflora* due to the competition for channels to enter the cell. The uptake of Cd by root was enhanced under iron deficiency for *Amaranthus mangostanus* (Zou et al., 2020) and *Oryza sativa* (Nakanishi et al., 2006). Similarly, we have demonstrated that sulfur can significantly improve the bioavailability of iron in the rhizosphere of *K. obovata* and enhance the tolerance of the plant to Cd contaminants in the surrounding (Li et al., 2017). The improvement of Fe bioavailability directly promoted the formation of iron plaque on the root surface. On the other hand, it improved the iron absorption and the process of competing with Cd for ion channels decreased the absorption of Cd by plants (Li et al., 2019a). Chromium, another highly biotoxic heavy metal element, in nature, the most stable and common valences of Cr are Cr(III) and Cr(VI). A trace level of Cr(III) (less than 1 mg/L) was reported to promote plant growth, while a higher available concentration may lead to the inhibition of biosynthesis and low biomass (Peralta-Videa et al., 2009). Meanwhile, Cr(VI) is generally more toxic to plants compared to Cr(III) due to its higher mobility in sediments and stronger oxidizability, which may damage root membranes and induce the formation of free radicals (Yu et al., 2017). Cr(III) enters plant tissues through passive mechanisms and is poorly translocated to aerial parts and accumulated in root tissues, while Cr(VI) is absorbed through active mechanisms and was reported to be hampered by the uptake of SO_4^{2-} and Ca^{2+} (González et al., 2014). In the study by Zandi et al. (2020) on rice, sulfur supply remarkably decreased the bioavailability of both Cr(III) and Cr(VI) by improving the barrier effect of iron plaque and competing for SO_4^{2-} carriers. Lead (Pb) also enters the roots passively via Ca^{2+} permeable channels, which indicates competition between Ca^{2+} and Pb^{2+} for channels to enter cells (Huang et al., 1996). However, the molecular level of uptake and

translocation mechanisms are still unknown. Moreover, like other heavy metals, the absorption of Pb is inhibited significantly by the iron plaque on the root surface (Ashraf et al., 2015).

In terms of the submicroscopic structure of plant cells, heavy metals may alter physiologic processes at the cellular and molecular level by displacing essential elements, blocking functional groups of molecules, inactivating enzymes, and damaging the structure of the membrane system (Fryzova et al., 2018). Heavy metal tolerance and detoxification strategies are presumably found in all coastal wetland plant species. Thiol-containing compounds, including cysteine, glutathione (GSH), and metallothionein (MT), are the keys to plant tolerance and detoxification (Fig. 5). Cysteine is initially synthesized in plant cells and then utilized as a precursor for synthesizing MT and GSH. MT is a family of cysteine-rich proteins that plays an important role in heavy metal immobilization due to its active thiol group (Fig. 5), and several studies have also shown that MTs can act as ROS scavenging enzymes (Yamauchi et al., 2017). GSH is a low molecular weight tripeptide, which eliminates excess ROS through the glutathione-ascorbate (GSH-AsA) pathway and alleviates the oxidative stress caused by heavy metals (Dai et al., 2017; Wu et al., 2021). Meanwhile, GSH is also the precursor for the synthesis of phytochelatin (PCs). PCs are thiol-rich peptides with the structure $(\gamma\text{-Glu-Cys})_n\text{-Gly}$, where n is generally between 2 and 5 (Negrin et al., 2017). Numerous studies showed that PCs bind heavy metals effectively through thiolate coordination and reduce their biotoxicity in cells (Dai et al., 2017; Nikalje and Suprasanna, 2018; Wu et al., 2020). Subsequently, heavy metal-PCs complexes are generally translocated to cell walls and vacuoles where metabolism is relatively inactive and minimizes the damage. Although the tissue distribution of heavy metals varies among different plant species, in general, wetland plants can fix most of the heavy metals in the below-ground roots to protect the above-ground tissues (leaves, stems, etc.). For example, the distribution of Cd concentration in *S. alterniflora* tissues was fine roots > inflorescences > rhizomes > stems > leaves (Chai et al., 2012); while in *P. australis* tissues was roots > rhizomes > leaves > stems (Bonanno and Giudice, 2010); roots > hypocotyls > stems and leaves for *K. obovata* (Weng et al., 2012); but, for *A. marina* the order was roots > stems > leaves (Li et al., 2019a). This may be due to the redistribution strategy in plant tissues in which heavy metals are complexed and immobilized by thiol-containing compounds like MTs and PCs in root cells. In summary, due to the active thiol groups, thiol-containing compounds are important factors that mediate plant cell tolerance to heavy metal stress and detoxification, participate in heavy metal fixation, translocation, and redistribution in plant tissues.

Additionally, in plant tissues, hydrogen sulfide (H_2S) is

considered a gaseous signal molecule. With the help of a flame photometric detector, plants were first detected to synthesize and emit H_2S by Wilson et al. (1978). In subsequent researches, H_2S was found to be a gasotransmitter that regulates diverse physiologic processes in plants. Previous reviews have summarized and discussed how H_2S mediates plant response to different abiotic stress (He et al., 2018; Hancock, 2019). Numerous studies have found that H_2S enhances plants' tolerance to heavy metal stress via the following pathways: inducing the activation of antioxidant enzymes and increasing antioxidant capacity (Mostofa et al., 2015); promoting low molecular weight organic acids secretion; alleviating ultrastructural changes (Ali et al., 2014); improving photosynthetic parameters and nutrient uptake; upregulating the GSH-AsA cycle (Singh et al., 2015); activating heavy metal chelators, and may react with heavy metals directly (He et al., 2018). However, recent studies have mainly focused on terrestrial crops (*Triticum aestivum*, *Hordeum vulgare*, *O. sativa*, etc.) and there is no research focus on coastal wetlands that have a relatively high H_2S emission (averaged at $0.035 \text{ g S/m}^2/\text{yr}$) due to the high SO_4^{2-} concentration and activity of SRB (Yu et al., 2019). As a result, to further understand the interaction between sulfur and heavy metals in different components and organizational levels, future work may focus on elaborating the effects and mechanisms of H_2S in regulating plant metabolism and stress tolerance in coastal wetlands contaminated by heavy metals.

4 Conclusions and future research directions

A thorough review of the literature reveals that coastal wetlands could function as either a “sink” or a “source” of heavy metals, which largely depends on environmental factors and conditions. In particular, sulfur plays a critical mediating role in the heavy metal cycle in coastal wetland ecosystems, affecting the speciation, transformation, and migration of heavy metals from sediments, rhizosphere, to vegetation and surrounding environments, and as well as regulating tolerance of plants to heavy metals.

To further understand the biogeochemical cycles of various biogenic elements in coastal wetlands, comprehensively assess the impact of human activities on coastal wetland ecosystems, and evaluate the potential fluctuations and risks, it is imperative to clarify the interactions between sulfur and heavy metals and their mechanisms from the different organizational levels and scales of coastal wetlands. Future studies are suggested on the following aspects:

- 1) Further explore the role and mechanisms of H_2S as a gaseous signal molecule, explain the mechanisms of H_2S -mediated heavy metal tolerance in coastal wetland plants. This could improve the knowledge of the interaction and mechanism between sulfur and heavy metals in plants.
- 2) Thus far, the interactions between sulfur and heavy metals in the rhizosphere are not fully understood. Studies are needed to elucidate the processes and mechanisms of

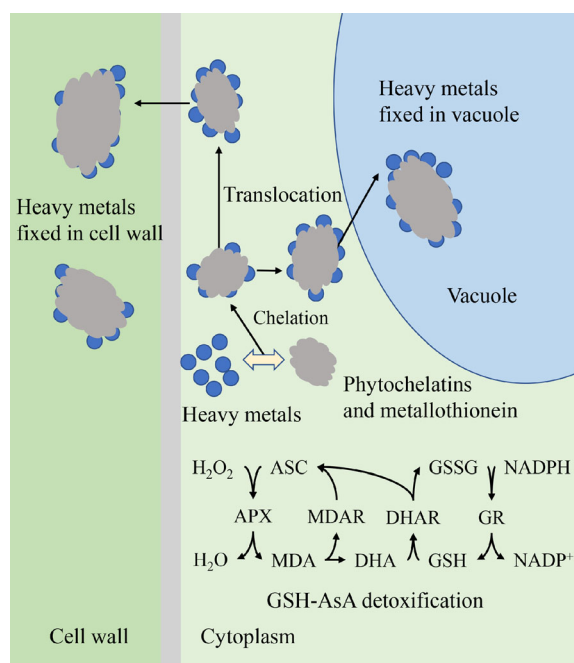


Fig. 5 Sulfur-containing compounds mediate heavy metal transport, immobilization and detoxification in plant cells.

various interactions among sulfur, heavy metals, plant roots, microbes, and other factors in the micro-interface between sediments and plants.

3) To systematically assess the environment of coastal wetlands, predict potential contamination risks, and improve management strategies, it is necessary to establish a dynamic biogeochemical cycle model of sulfur and heavy metals in coastal wetlands on a macro and even global scale using big data from field studies and machine learning technology.

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